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RESEARCH ARTICLE

Vertical distribution and structure of copepod (Arthropoda: Copepoda) assemblages in two different seasons down to 1,200 m in the tropical Southwestern Atlantic

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ABSTRACT. The vertical distribution of copepod assemblages, ascertained from the surface down to 1,200 m, was investigated during two sampling periods (rainy and dry seasons), at four depths, in the oligotrophic waters of the southwestern Atlantic Ocean. Total density, diversity, and richness differed among sampling depths. Copepod density decreased with depth in the two sampling periods, with a maximum at 1 m and a slight decrease at 800 m. Higher diversities were observed at 250 m and 1,200 m during the rainy season and at 1 m and 1,200 m during the dry season. The maximum number of species was found at 1,200 m during the rainy season and at 1 m during the dry season. Various copepod assemblages were delimited in the water column in the two sampling periods. The deeper copepod assemblages occupied a wider range of depths. Salinity and temperature influenced the structure of copepod assemblages and reflected the hydrographic characteristics of the water masses in the region. *Candacia pachydactyla* (Dana, 1849), *Scolecithrix danae* (Lubbock, 1856), and *Agetus limbatus* (Brady, 1883) were the indicator species found at 1 m. The effects of different environmental factors on the copepod assemblages suggest that these consortia occupy distinct niches in the ocean.

KEY WORDS. Mesozooplanktonic copepod, Southeastern Brazil, Tropical environment.

INTRODUCTION

Oligotrophic regions are more productive and dynamic than previously thought, and have a high degree of biological variability (Dias et al. 2015). Oligotrophic areas constitute more than 75% of oceanic surfaces. They may play a significant role in oceanic biogeochemical budgets and global elemental cycling (Dufour et al. 1999, Corno 2006 and references therein). The southwest Atlantic Ocean is one of the most oligotrophic areas of all oceans worldwide (Andrade et al. 2007).

In zooplankton communities, copepods are known for their diversity and importance in the food web. They are the most abundant primary consumers in the ocean and the main food source for several planktophagous fishes (such as herring, anchovy, sardine, and corvine), fish larvae, and planktonic- and benthic invertebrates (Björnberg 1981).

Unlike other oceanic regions of the southern hemisphere, the southwestern Atlantic Ocean has seldom been qualitatively studied to obtain biogeographical data on zooplankton dynamics, particularly in external slope areas. Most studies in this region have been performed within the uppermost meters of the water column (e.g. Björnberg 1963, Valentin 1984a, b, Campaner 1985, Valentin et al. 1987, Dias 1996, Bassani et al. 1999, Lopes et al. 1999, Bonecker 2006, Lopes et al. 2006, Bonecker et al. 2007, Dias et al. 2015). These studies examined zooplankton (mainly copepod) composition, abundance, distribution, and biomass and have demonstrated the influence of hydrography on spatial variability. The deep sea zooplankton on the Brazilian central coast has not been investigated in detail. Information on the mesopelagic and bathypelagic communities is scarce except for that reported by Bonecker et al. (2014) and Dias et al. (2010). These authors described the compositions of

the mesozooplankton and copepod communities, respectively. The sampling range in both cases was from 0 to 2,300 m depth.

The aims of this study were as follows: (a) describe the vertical variation in copepod density and assemblage structure (composition, richness, and diversity) down to 1,200 m over two seasons in the southwest Atlantic Ocean; (b) determine whether copepod population characteristics and environmental parameters are correlated; and (c) investigate copepod assemblages using indicator species. The hypothesis was that copepod assemblages are formed by characteristic indicator species groups arranged along a vertical gradient determined by oceanographic conditions.

MATERIAL AND METHODS

The Campos Basin is located between 20.5°S and 24°S off the central Brazilian coast and covers an area of approximately 100,000 km². In this region, the mean continental shelf width is 100 km and the shelf break is located between the 80-m and 130-m isobaths in the northern- and southern portions, respectively. The slope extends over a width of 40 km and has a mean declivity of 2.5°. Its base is shallower at the northern limit (about 1,500 m) and deeper near the southern limit (about 2,000 m) (Viana et al. 1998). The regional climate is warm and humid with a rainy summer season from November to February and a dry winter season from June to August (Lacerda et al. 2004).

The Brazilian coast is influenced by the warm, oligotrophic Brazil Current, which is a western boundary and flows from the northeast toward the southwest. It forms part of the South Atlantic western boundary current system (Stramma et al. 1990). The Campos Basin is characterized by its water column structure and water mass distributions over the continental shelf and slope. This region has various water masses each with distinct temperatures, salinities, and dissolved oxygen (DO) levels that provide different habitats for pelagic species (Fig. 1). The upper depths include the nutrient-poor subsurface water (Tropical Water, TW) and the relatively cold, nutrient-rich South Atlantic Central Water (SACW, 142–567 m depth). Their temperatures and salinities are below 20 °C and 36.4, respectively (Mémery et al. 2000, Silveira et al. 2000, Pedrosa et al. 2006). Water masses at lower depths include the Antarctic Intermediate Water (AAIW, 567–1,060 m), the Upper Circumpolar Deep Water (UCDW, 1,060–1,300 m), and the North Atlantic Deep Water (NADW, 1,300–3,260) (Viana et al. 1998, Pedrosa et al. 2006, Bonecker et al. 2014).

Mesozooplankton (length >200 µm) samples were collected during oceanographic cruises from February 25-April 13, 2009 (rainy season, RS) and from August 5 to September 17, 2009 (dry season, DS). The sampling stations were distributed along six transects perpendicular to the coast (A, C, D, F, H, and I) in a north-south direction. Each transect contained four sampling stations on the slope between the 400-m and 3,000-m isobaths (400 m, 1,000 m, 1,900 m, and 3,000 m; Fig. 2). Zooplankton samples were not collected in transects B, E, and G. All samples

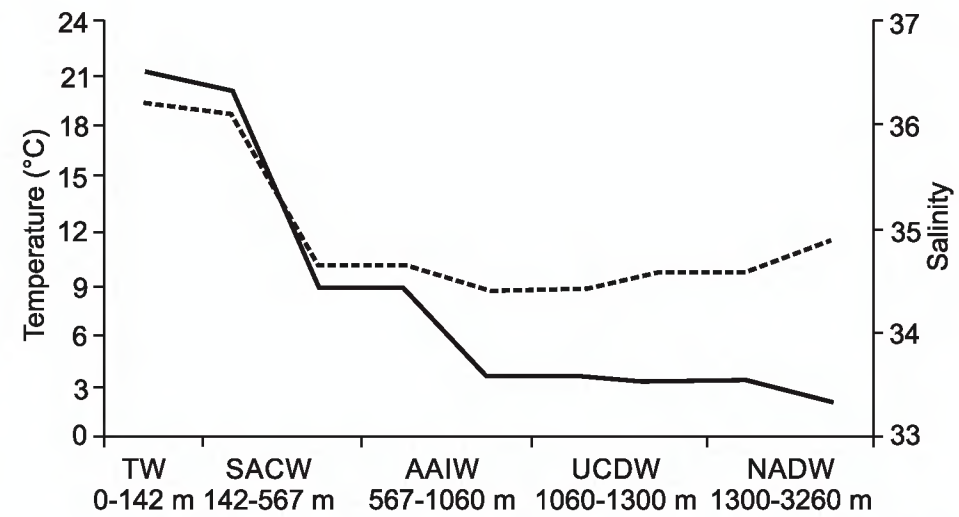

Figure 1. Salinity and temperature of the five water masses (0–3260 m) in the Campos Basin, central Brazilian coast, modified from Bonecker et al. (2014). Solid line = temperature; dashed line = salinity; SS, Subsurface Water; SACW, South Atlantic Central Water; AAIW, Antarctic Intermediate Water; UCDW, Upper Circumpolar Deep Water; NADW, North Atlantic Deep Water.

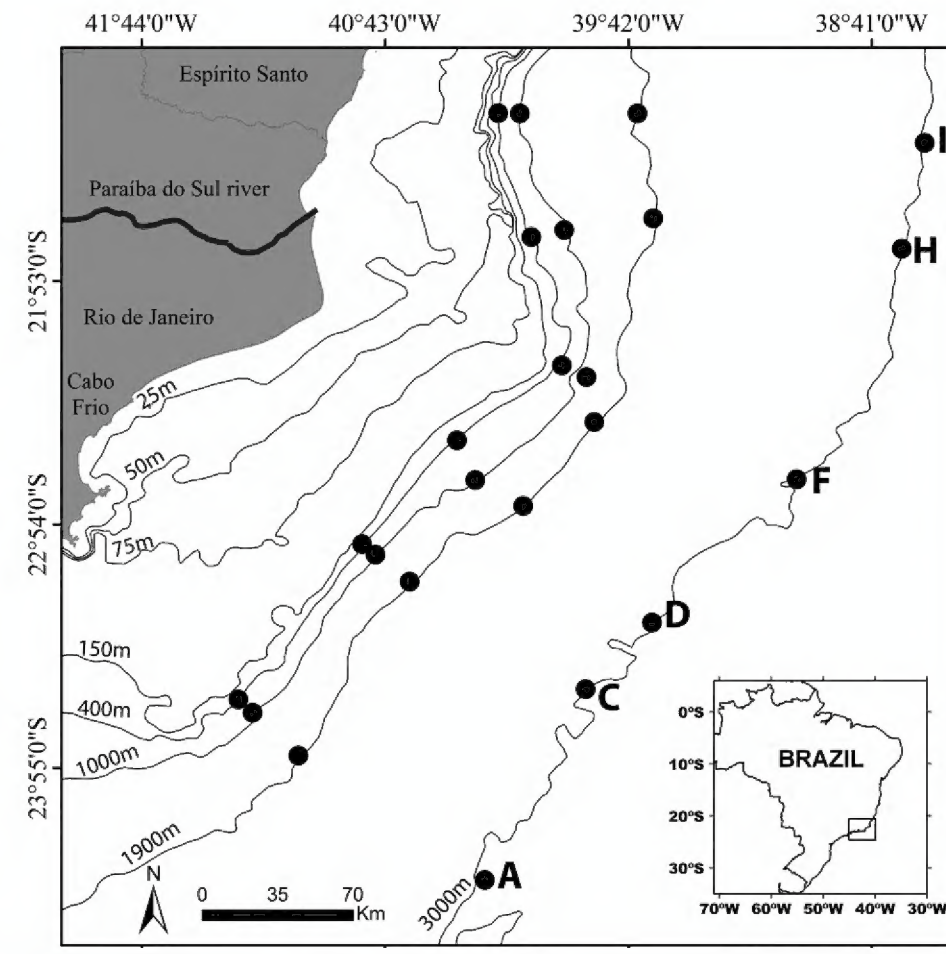

Figure 2. Study area showing sampling stations.

were collected between 6:18 pm and 5:08 am during the rainy season and between 5:57 pm and 5:46 am during the dry season (local time).

Environmental data included (a) water temperature and salinity at all sampling depths, namely, 1 m, 250 m, 800 m, and 1,200 m, by using a CTD (sonde); (b) inorganic nutrients, determined by standard oceanographic methods (Grasshoff et al. 1999); (c) DO, measured continuously in the water column with a sensor coupling in the CTD; and (d) suspended particulate matter (SPM), obtained from water sample filtration. Detailed

methodology and discussion of the hydrochemistry of the study area are presented elsewhere (Rodrigues et al. 2014, Dias et al. 2015, Suzuki et al. 2015).

Mesozooplankton samples were collected by horizontal hauls in the previously named water mass nuclei (Tropical Water [TW, 1 m], South Atlantic Central Water [SACW, 250 m], Antarctic Intermediate Water [AAIW, 800 m], and Upper Circumpolar Deep Water [UCDW, 1,200 m]). The horizontal hauls in the slope were taken at 2 knots for 10 min or until the filtered water volume reached 50 m^3. Hauls were made using a MultiNet type midi (Hydro-Bios, Altenholz, Germany, 200 µm white mesh, 50 × 50 frame opening) fitted with a digital flowmeter attached to the inner net mouth and an external meter to assess filtration efficiency. Different nets were used at each depth to prevent sample cross-contamination. The MultiNet was also fitted with a depth gauge. Both the depth and water volume were transmitted to a computer along with the hauls. In the dry season, no samples were collected from the 3,000-m isobath of transects H and I due to logistical problems. A total of 145 samples were analyzed: 78 in the rainy season, and 67 in the dry season.

Samples were fixed and preserved in 4% buffered formalin. In the laboratory, the preserved samples were divided into 1–10 fractions with a Folsom Plankton Splitter (Hydro-Bios) (McEwen et al. 1957) and the resultant subsamples analyzed. All copepods were sorted, identified, and counted under a stereoscopic microscope according to the methods of Bradford-Grieve et al. (1999) and Dias and Araujo (2006). Taxon abundance per cubic meter and copepod species composition were determined for all samples. The total abundance of each species was estimated from both adult and juvenile forms. All specimens were deposited in the copepod collection of the Integrated Zooplankton and Ichthyoplankton Laboratory of the Federal University of Rio de Janeiro (DZUFRJ Copepoda 12622-12631, DZUFRJ Copepoda 12791-12952, DZUFRJ Copepoda 13058-14020, DZUFRJ Copepoda 14059-14189, DZUFRJ Copepoda 14618-14715, DZUFRJ Copepoda 14726-14760, DZUFRJ Copepoda 14834-14975, DZUFRJ Copepoda 15024-15509, DZUFRJ Copepoda 15560-15892, and DZUFRJ Copepoda 16316-16895).

The Shannon-Wiener diversity index (H') and richness were calculated for each station during the sampling period to identify any differences in biodiversity. Pielou's index of evenness was also determined. The Shannon-Wiener diversity index was calculated as follows: $H' = -\sum pi * \ln (pi)$, where pi is the fraction of species i in the total sample. These analyses were run using PRIMER v. 6.1 (Clarke and Gorley 2006). Vertical depth differences in copepod density, richness, diversity, and evenness were tested using generalized linear models (GLM) with gamma family (dispersion = 1). A low additive constant (1) was applied to the copepod density density and evenness data in each sampling station to eliminate zero values in the matrix because the gamma family does not allow for zeros. The analyses were performed using R v. 3.1.3 (R Core 3 Team 2015).

"Station x copepod species" matrices (sampling depths as rows, and copepod species density at each station as columns) were analyzed for each sampling period. Species with occurrences of > 1% and the [log(x + 1)] transformed density data were used to generate a Bray-Curtis similarity matrix. The following multivariate techniques were used to identify various copepod assemblages: (1) an analysis of similarity (ANOSIM) was used to assess whether the copepod assemblage structure varied with depth; (2) a similarity of percentages (SIMPER) analysis was used to identify the species that contributed most to the similarities within groups; and (3) an indicator species analysis (ISA) was used to identify the indicator copepod species at each sampling depth (Dufrêne and Legendre 1997, De Cáceres and Legendre 2009). The ISA index is at a maximum (100%) when all exemplary species are found in a single sample group and the species occurs in all samples from that group. A species was considered an indicator in a particular water mass when its ISA value was significantly higher than that expected by chance alone (compared to one thousand random samples from plots with the same number of species occurrences) and higher than 70%. These indicator values were checked by the Monte Carlo test to establish reliable significance levels (IV,% of perfect indication, $p < 0.05$) The ANOSIM and SIMPER analyses were performed using PRIMER v. 6.1 (Clarke and Gorley 2006). The ISA was carried out using PC-ORD for Windows v. 5.0 (MjM Software, Gleneden Beach, Oregon, USA) (McCune and Mefford 1999).

The relationship between variations in copepod assemblage structure and environmental parameters (temperature, salinity, suspended particulate matter, DO, nitrate, silicate, and inorganic-P or orthophosphate) during the sampling period was analyzed by distance-based linear models (DistLM). The Akaike information criterion for small samples (AICc) was used to select the best model. A distance-based redundancy analysis (dbRDA) was performed to represent the best model selected by DistLM. Both DistLM and dbRDA were performed in PRIMER v. 6.1 (Clarke and Gorley 2006) and PERMANOVA+ for PRIMER (Anderson et al. 2008). All analyses were performed using the matrix for both sampling periods. The results were considered significant when $p < 0.05$.

RESULTS

Hydrography conditions

The environmental conditions during the study period were described in detail by Rodrigues et al. (2014), Dias et al. (2015), and Suzuki et al. (2015). Therefore, they are only briefly summarized here and in Table 1. The lowest temperature and salinity values were obtained during the dry season. At 800 and 1,200 m, both temperature and salinity were relatively uniform. The suspended particulate matter (SPM) ranged from 0.01 mg L^{-1} at 800 m to 4.19 mg L^{-1} at 1 m in the rainy and dry season, respectively. The DO values were homogeneous in both sampling seasons except at 1 m. In both sampling periods, the highest nutrient concentrations were observed in the deepest waters.

Table 1. Minimum and maximum values recorded for temperature (°C), salinity, suspended particulate matter (SPM, mg L^{-1}), dissolved oxygen (DO, mg L^{-1}), nitrate (µmol L^{-1}), silicate (µmol L^{-1}), and orthophosphate (µmol L^{-1}) in samples collected in the Campos Basin water column during the rainy- and dry seasons of 2009. RS, rainy season; DS, dry season.

Depth	Sampling Periods	Temperature		Salinity		SPM		DO		Nitrate		Silicate		Orthophosphate	
		Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max
1 m	R.S.	36.68	37.28	25.96	28.50	0.29	1.82	5.78	6.38	0.56	2.19	0.41	9.06	0.01	0.08
	D.S.	36.26	37.12	21.19	24.89	0.15	4.19	4.36	7.14	0.37	4.85	0.39	7.89	0.02	0.44
250 m	R.S.	35.28	35.99	13.64	25.65	0.04	1.93	6.17	6.68	0.58	7.67	0.58	3.53	0.02	0.71
	D.S.	35.12	35.79	12.09	16.75	0.17	0.87	6.22	6.77	1.48	11.41	1.35	7.15	0.26	0.81
800 m	R.S.	34.33	34.40	4.64	5.61	0.01	1.02	6.03	6.84	5.29	32.37	5.33	30.15	0.72	2.00
	D.S.	34.34	34.46	4.39	5.33	0.22	0.67	6.08	6.60	18.18	34.72	19.85	31.31	1.69	1.95
1,200 m	R.S.	34.45	34.57	3.20	3.53	0.33	1.11	5.90	6.06	17.58	31.76	20.93	51.11	1.71	2.08
	D.S.	34.54	34.64	3.21	3.42	0.13	1.05	5.76	5.86	25.42	35.33	37.54	49.88	1.87	2.07

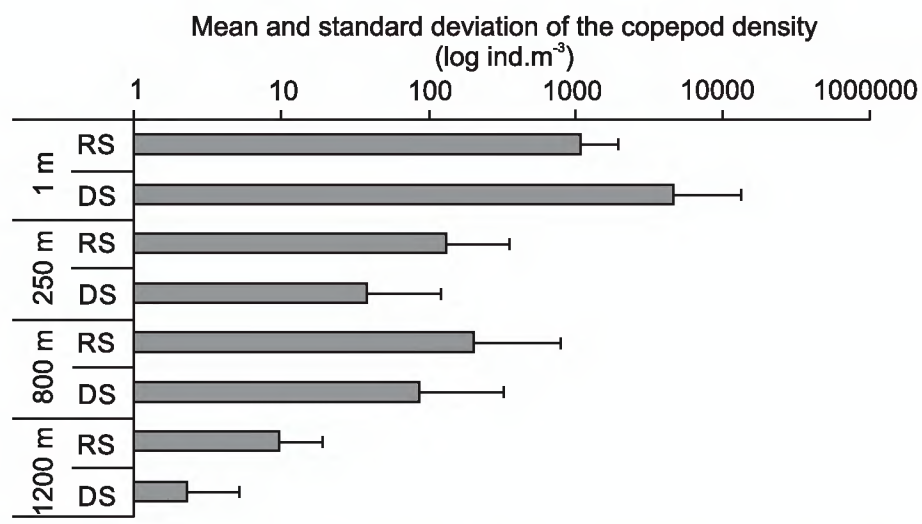

Figure 3. Vertical distribution of the mean and standard deviation of the copepod density (log ind.m^{-3}) during two sampling periods: rainy season, RS; dry season, DS.

Abundance, biodiversity, spatial comparisons, and composition

The total copepod density varied among the sample depths ($p < 0.05$). The highest values were recorded during the rainy season except at 1 m where the copepod density was higher during the dry season than the rainy season (Fig. 3). The vertical pattern showed that copepod density decreased with depth during both sampling periods. The highest densities were observed at 1 m (Mean: RS, 1,102.44 ± 844.03 ind.m^{-3}; DS, 4,593.63 ± 8,743.59 ind.m^{-3}) and at 800 m (Mean: RS, 205.41 ± 585.87 ind.m^{-3}; DS, 86.18 ± 232.34 ind.m^{-3}). The lowest densities were observed at 1,200 m (Mean: RS, 8.52 ± 7.98 ind.m^{-3}; DS, 1.29 ± 1.93 ind.m^{-3}) (Fig. 3).

A total of 139 species were identified in the Campos Basin over both seasons: 111 calanoids, 18 poecilostomatoids, 6 harpacticoids, and 4 cyclopoids. The calanoid order was the most abundant in both sampling periods. It constituted 66–87% of the total copepod density (1 m: 76%; 250 m: 2%; 800 m: 4%; and 1,200 m < 0.05%). Poecilostomatoids (14% of the total copepod density) were the most abundant at 1 m and at 250 m. They were represented primarily by the Oncaeidae and Corycaeidae families, which were relatively abundant at 1,200 m. In both sampling periods, the cyclopoid copepods identified came exclusively from the Oithonidae family, and the genus *Oithona* Baird, 1843 was more abundant in 250 m. Harpacticoid copepod density peaked at 1 m and was represented mainly by *Macrosetella gracilis* (Dana, 1847). In the mesobathypelagic region (250–800 m), the harpacticoids *Aegisthus* spp. predominated, but their abundance was low compared to that of other genera. Cyclopoid and harpacticoid copepods made up 1–1.5% of the copepod density in both sampling periods (Suppl. materials 1, 2).

Higher diversity values were observed at 250 and 1,200 m in the rainy season and at 1 m and 1,200 m in the dry season. Significant differences in diversity were found across sample depths ($p < 0.05$). Diversity was lower at 800 m (Fig. 4). The maximum number of species was found at 1,200 m during the rainy season (21) and at 1 m during the dry season (17) (Fig. 4). As for total density and diversity, richness differed significantly across water masses ($p < 0.05$). Mean evenness ranged from 0.97 (1 m) to 0.87 (1,200 m) during the rainy season and from 0.98 (1 m) to 0.83 (800 m) during the dry season (Fig. 4). The evenness also differed significantly across sample depths ($p < 0.05$).

Seven copepod species were abundant during the rainy season: *Undinula vulgaris* (Dana, 1849), *Clausocalanus furcatus* (Brady, 1883), *Acrocalanus longicornis* Giesbrecht, 1888, *Paracalanus quasimodo* Bowman, 1971, *Temora stylifera* (Dana, 1849), *Oncaea venusta* Philippi, 1843, and *Farranula gracilis* (Dana, 1849). These constituted 68% of the total copepod density. In the dry season, thirteen species predominated, and represented 86% of the total copepod density: *Calanoides carinatus* (Krøyer, 1849), *C. furcatus*, *Centropages velificatus* (Oliveira, 1947), *Lucicutia flavicornis* (Claus, 1863), *A. longicornis*, *P. quasimodo*, *Rhincalanus cornutus* (Dana, 1849), *Subeucalanus pileatus* (Giesbrecht, 1888), *Temora turbinata* (Dana, 1849), *T. stylifera*, *Oithona plumifera* Baird, 1843, *O. venusta*, and *Onchocorycaeus giesbrechti* (Dahl F., 1894) (Table 2). Contributions of the most representative species varied at the different sampling depths as follows: *C. furcatus*, *F. gracilis*, *P. quasimodo*, and *T. stylifera* (1 m); *O. venusta*, *Scolecithricella minor* (Brady, 1883), *Ctenocalanus vanus* Giesbrecht, 1888, and *Oithona similis* Claus, 1866 (250 m);

Table 2. Vertical distribution of the mean (standard deviation) density (ind.m^{-3}) of the 20 most abundant copepods species found in Campos Basin. RS, rainy season; DS, dry season.

Species	1 m		250 m		800 m		1,200 m	
	RS	DS	RS	DS	RS	DS	RS	DS
Calanoides carinatus	0.27 (1.30)	126.51 (499.99)	1.71 (7.00)	0.72 (3.18)	16.17 (30.56)	31.16 (105.22)	0.13 (0.36)	0.28 (0.04)
Nannocalanus minor	29.99 (76.58)	32.98 (104.26)	0.98 (2.18)	0.06 (0.19)	0.14 (0.31)	0.20 (0.76)	0.16 (0.23)	< 0.01 (< 0.01)
Undinula vulgaris	69.34 (134.22)	39.35 (139,42)	1.51 (3.68)	0.04 (0.13)	0.23 (0.62)	< 0.01 (0.01)	0.17 (0.30)	0.02 (0.01)
Clausocalanus furcatus	132.82 (99.76)	1,139.59 (2,805.30)	4.10 (7.18)	0.38 (1.00)	0.78 (1.81)	0.76 (2.63)	0.72 (1.53)	1.66 (0.41)
Ctenocalanus citer	–	7.76 (34.95)	0.37 (1.83)	< 0.01 (0.02)	42.07 (172.15)	3.26 (12.22)	–	–
Ctenocalanus vanus	–	6.28 (28.47)	0.34 (1.64)	2.51 (10.72)	46.76 (123.43)	0.57 (2.18)	0.12 (0.22)	–
Centropages velificatus	0.13 (0.47)	115.41 (524.23)	–	0.15 (0.72)	–	0.12 (0.38)	–	0.05 (0.01)
Lucicutia flavicornis	219 (5.99)	49.94 (113.34)	0.53 (0.81)	0.32 (0.61)	0.04 (0.10)	< 0.01 (0.02)	0.23 (0.43)	0.02 (0.03)
Acrocalanus longicornis	50.28 (44.69)	62.43 (162,69)	0.59 (1.76)	–	0.27 (0.63)	< 0.01 (0.01)	0.05 (0.13)	–
Calocalanus pavoninus	21.77 (34.57)	19.43 (58,56)	0.39 (1.53)	< 0.01 (0.02)	0.10 (0.25)	< 0.01 (0.01)	0.08 (0.14)	–
Paracalanus quasimodo	68.62 (185.07)	296.29 (610.22)	3.70 (17.54)	0.56 (2.25)	< 0.01 (0.01)	0.09 (0.33)	0.02 (0.06)	–
Rhincalanus cornutus	1.36 (5.06)	47.32 (148.26)	0.14 (0.38)	0.02 (0.06)	0.03 (0.06)	0.51 (1.51)	< 0.01 (0.02)	< 0.01 (< 0.01)
Subeucalanus pileatus	–	45.58 (175.51)	–	0.01 (0.05)	0.10 (0.41)	0.02 (0.05)	–	< 0.01 (0.02)
Temora turbinata	–	111.72 (419.15)	–	0.20 (0.71)	–	0.10 (0.26)	0.02 (0.07)	< 0.01 (0.01)
Temora stylifera	80.97 (109.87)	221.94 (575.14)	3.38 (8.58)	0.05 (0.23)	0.43 (0.80)	0.03 (0.12)	0.10 (0.19)	0.01 (0.02)
Oithona plumifera	2.78 (6.87)	47.91 (115.36)	0.18 (0.57)	1.24 (3.59)	–	0.20 (0.54)	0.05 (0.09)	0.04 (0.07)
Oncaea venusta	80.65 (75,70)	162.50 (278.93)	12.90 (20.78)	5.87 (19.05)	2.34 (3.57)	0.81 (2.25)	1.15 (1.98)	0.24 (0.49)
Onychocorycaeus giesbrechti	24.60 (36.49)	79.38 (219.82)	0.11 (0.27)	0.07 (0.19)	0.005 (0.02)	0.02 (0.06)	0.07 (0.20)	–
Farranula gracilis	204.93 (222.99)	37.12 (51.74)	3.88 (9.51)	0.02 (0.07)	0.60 (0.82)	0.65 (2.44)	0.59 (0.94)	0.03 (0.06)
Macrosetella gracilis	37.31 (99,12)	11.87 (41.39)	3.60 (6.73)	0.27 (0.71)	0.15 (0.25)	0.11 (0.38)	0.32 (0.44)	0.02 (0.01)

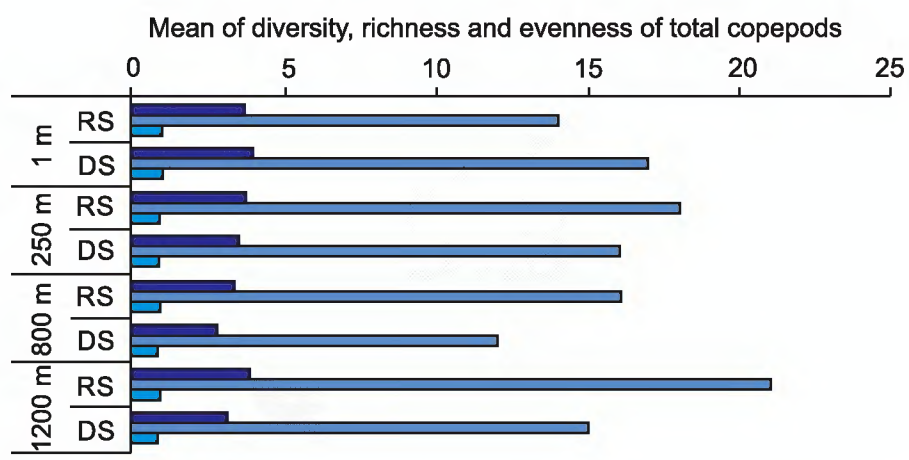

Figure 4. Vertical distribution of the mean diversity, species richness, and evenness of total copepods in the Campos Basin: dark blue bars, diversity; cobalt bars, richness; cyan bar, evenness. RS, rainy season; DS, dry season.

C. carinatus, *Ctenocalanus citer* Heron & Bowman, 1971, and *C. vanus*, (800 m); *O. venusta*, *C. furcatus*, *Conaea rapax* Giesbrecht, 1891, and *F. gracilis* (1,200 m).

Spatial characterization of the copepod assemblages

The similarity analysis revealed that variations in species density were important in determining changes in copepod assemblages along the depths. Pairwise ANOSIM tests during the rainy season demonstrated that sampling depth groups were separated according to their copepod assemblages except for 800 m and 1,200 m (ANOSIM: p = 0.1%; global R = 0.662; Table 3).

The copepod species that contributed most to the similarity of the copepod assemblages at 1 m, 250 m, and 800–1,200 m (SIMPER test) are shown in Table 4. *Oncaea venusta* participated in the copepod assemblages at all depth groups. *Clausocalanus furcatus* and *T. stylifera* occurred in the 1 m, 250 m, and 800–1,200 m assemblages. *F. gracilis* was detected in the 1 m, and 800–1,200 m copepod assemblages. In the 250 m assemblage, *O. similis*, *Triconia* cf. *conifera* (Giesbrecht, 1891), *Lubbockia squillimana* Claus, 1863, *Pleuromamma abdominalis* (Lubbock, 1856), *L. flavicornis*, and *Pleuromamma gracilis* Claus, 1863 were also present. At 800–1,200 m, *C. carinatus*, *T.* cf. *conifera*, and *C. vanus* contributed to the formation of the copepod assemblage.

During the dry season, pairwise ANOSIM tests indicated that the structures of the copepod assemblages at 1 m and at 250 m were distinct from the others (ANOSIM: p = 0.1%; global R = 0.673; Table 3).

The copepod species that contributed most to the similarity of the copepod assemblages at 1 m, 250 m, and 800–1,200 m (SIMPER test) are shown in Table 5. *Clausocalanus furcatus* and *O. venusta* contributed most (>30% similarity) to the formation of the 1 m, 250 m, and 800–1,200 m copepod assemblages. *Farranula gracilis* also contributed to the 1 m assemblage. At 250 m, *T.* cf. *conifera* and *Heterorhabdus spinifrons* (Claus, 1863) contributed the most (along with *O. venusta*) to the formation

Table 3. Analyses of similarity (ANOSIM) between sampling depth groups during the rainy and dry seasons. R, strength of the difference between groups (* significant differences, $p < 0.05$).

Groups of sampling depths	R Statistic	
	Rainy season	Dry season
1 m x 250 m	0.689*	0.759*
1 m x 800 m	0.774*	0.789*
1 m x 1,200	0.951*	0.986*
250 m x 800 m	0.365*	0.359*
250 m x 1,200 m	0.474*	0.547*
800 m x 1,200 m	0.087	0.024

Table 4. Copepod species and their contribution (%) to the similarity of assemblages obtained during the rainy season through the SIMPER analysis.

1 m		250 m		800–1,200 m	
Species	(%)	Species	(%)	Species	(%)
Farranula gracilis	17.48	*Oncaea venusta*	27.45	*Oncaea venusta*	23.02
Clausocalanus furcatus	14.80	*Oithona similis*	14.71	*Calanoides carinatus*	9.93
Oncaea venusta	13.93	*Triconia* cf. *conifera*	7.32	*Clausocalanus furcatus*	9.93
Acrocalanus longicornis	9.69	*Macrosetella gracilis*	6.46	*Triconia* cf. *conifera*	8.42
Undinula vulgaris	9.38	*Oncaea media*	5.47	*Farranula gracilis*	6.68
Temora stylifera	9.10	*Clausocalanus furcatus*	5.20	*Conaea rapax*	4.91
Nannocalanus minor	4.97	*Lubbockia squillimana*	3.47	*Ctenocalanus vanus*	3.69
Others	20.65	*Pleuromamma abdominalis*	2.80	*Undinula vulgaris*	3.37
		Lucicutia flavicornis	2.64	*Temora stylifera*	3.15
		Temora stylifera	2.50	*Macrosetella gracilis*	3.05
		Pleuromamma gracilis	2.26	*Oithona similis*	2.97
		Others	19.72	Others	20.88

of the assemblage *C. rapax* and *C. carinatus* also appeared in the copepod assemblages at 800–1,200 m.

The Indicator Species Analysis identified indicator species only to 1 m depth ($p < 0.05$). They were *Candacia pachydactyla* (Dana, 1849), *Scolecithrix danae* (Lubbock, 1856), and *Agetus limbatus* (Brady, 1883), with indicator values ≥ 88.8%, and all of which occurred in the low-density samples.

Relationship between structure of copepod assemblages and environmental parameters

During the sampling period, the best model (DistLM, AIC = 1,128.4, $R^2 = 0.212$) captured 81.5% of the variability in the fitted model and 16.9% of the variability in the dataset (first two dbRDA axes in Fig. 5). The model included two variables: salinity and temperature, Salinity explained 17% of the variability in copepod assemblage structure. The first dbRDA axis is directly correlated to salinity and temperature. The second dbRDA axis

Table 5. Copepod species and their contribution (%) to the similarity of assemblages obtained during the dry season through the SIMPER analysis.

1 m		250 m		800 m – 1,200 m	
Species	(%)	Species	(%)	Species	(%)
Clausocalanus furcatus	21.03	*Oncaea venusta*	35.81	*Oncaea venusta*	27.63
Oncaea venusta	14.3	*Triconia* cf. *conifera*	17.72	*Conaea rapax*	14.26
Farranula gracilis	8.94	*Heterorhabdus spinifrons*	4.96	*Calanoides carinatus*	13.50
Paracalanus quasimodo	8.20	*Macrosetella gracilis*	4.20	*Clausocalanus furcatus*	12.28
Temora stylifera	6.69	*Oithona setigera*	4.04	*Macrosetella gracilis*	6.58
Undinula vulgaris	4.62	*Oithona plumifera*	3.67	*Triconia* cf. *conifera*	4.31
Lucicutia flavicornis	4.37	*Oncaea media*	3.64	Others	21.44
Onchocorycaeus giesbrechti	3.86	*Scolecithricella minor*	2.92		
Acrocalanus longicornis	2.71	*Clausocalanus furcatus*	2.50		
Nannocalanus minor	2.63	Others	20.54		
Triconia cf. *conifera*	2.54				
Macrosetella gracilis	2.32				
Others	17.79				

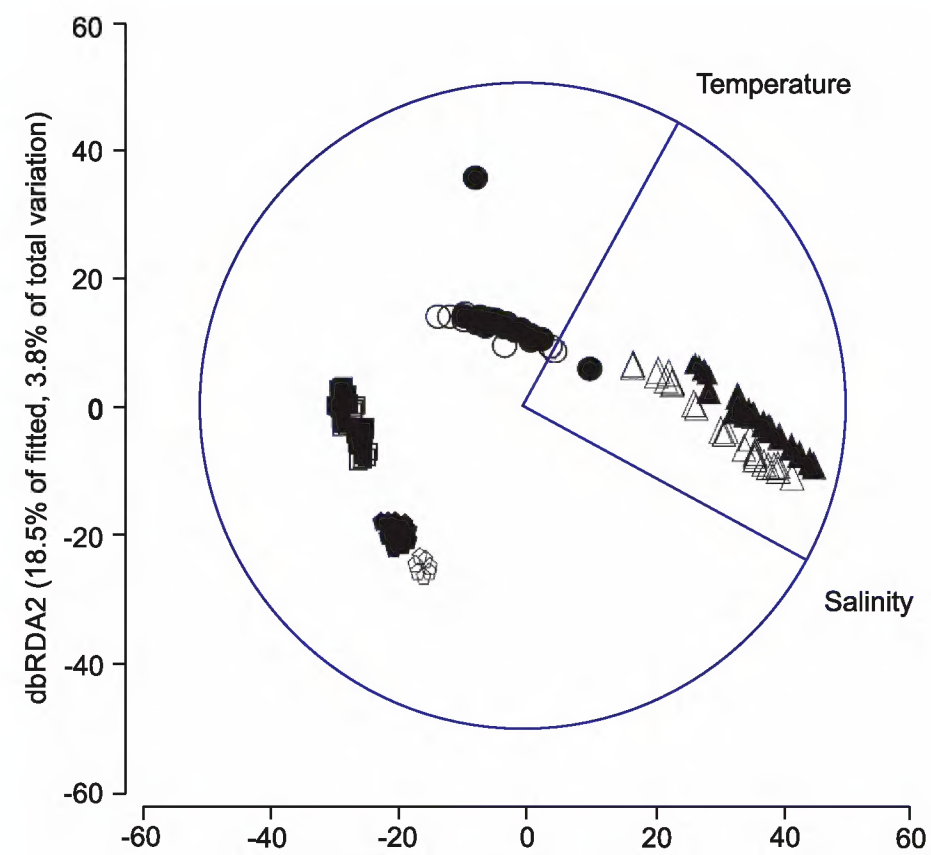

Figure 5. DbRDA ordination derived from DistLM analysis, including the main environmental parameters explaining the variability in copepod assemblage structures during the sampling period. Temp, temperature; Sal, salinity. Black triangle, rainy season 1 m; open triangle, dry season 1 m; black circle, rainy season 250 m; open circle, dry season 250 m; black square, rainy season 800 m; open square, dry season 800 m; black polygon, rainy season 1,200 m; open polygon, dry season 1,200 m.

is directly correlated to temperature and inversely correlated to salinity. The first dbRDA axis separated the assemblages sampled at 1 m and 250 m, and the deep assemblages (800 m and 1,200 m). The second axis discriminated the assemblages sampled at the lower depths. The 800 m and 1,200 m assemblages are separated in the plot below.

DISCUSSION

Hydrography conditions

The environmental parameters described along the water column reflect the hydrological characteristics of the water masses in this region (Niencheski et al. 1999, Rezende et al. 2007). Temperature and salinity values recorded in the area decreased from the subsurface (1 m) down to deep water (1,200 m). The inorganic nutrient concentrations had a vertical distribution pattern typical of oceanic regions, namely, increasing from the surface to deeper waters. The nutrient concentrations recorded in the surface layer of the Campos Basin are characteristic of oligotrophic waters found in the Brazil Current. They are indicative of the low primary production in the oceanic region (Metzler et al. 1997). Deep waters are more enriched especially along the continental margin of southeastern Brazil. Nutrients are added when the surrounding currents remobilize sediment (Silveira et al. 2000, Suzuki et al. 2015).

Abundance, biodiversity, spatial comparisons, and copepod assemblage composition

Copepod density and diversity distinguished the shallowest (1 m) and deepest (250–1,200 m) waters during both sampling periods. In both seasons, the total abundance decreased with depth except for a slight increase at 800 m. Richness and diversity increased in the mesopelagic and bathypelagic regions. Dusk-to-dawn sampling in the present study may have introduced bias in the data due to the diel vertical zooplankton migration. Nevertheless, other studies showed patterns similar to those observed here. Vinogradov et al. (1998) found copepod richness maxima at mesobathypelagic depths in both daytime- and nighttime vertical hauls (0–3,774 m) in the frontal zone between the Gulf Stream and the Labrador Current. In another study in the subtropical and subarctic North Pacific Ocean, Steinberg et al. (2008) noted density peaks at the surface and in the mesopelagic zone in both day and night vertical hauls (0–1,000 m). The authors attributed the density trend to the presence of a very high number of taxa feeding on suspended or sinking detritus in the mesopelagic zone and the occurrence of a large population of ontogenetically migrating calanoid copepods. In the present study, the abundance of large copepods – *C. carinatus*, *R. cornutus*, *Undeuchaeta plumosa* (Lubbock, 1856), *Heterorhabdus papilliger* (Claus, 1863), *Pleuromamma* spp. Giesbrecht & Schmeil, 1898, and *Lophothrix latipes* (Scott T., 1894) – and cold water species (*C. citer*) in deep waters may account for the observed vertical abundance and diversity patterns.

Although vertical hauls were used at the greatest depths, the very low density, richness, and diversity values found at 1,200 m follow the same trend reported in vertical studies of the southwestern Atlantic Ocean (Dias et al. 2010, Bonecker et al. 2014). In the oligotrophic Levantine Sea of the Eastern Mediterranean, Weikert et al. (2001) also observed this pattern for deep-sea plankton communities sampled in daytime- and nighttime hauls (0–4,175 m).

Most of the copepods species observed in this study were previously reported for the oceanic waters of Brazil (Gusmão et al. 1997, Lopes et al. 1999, Cavalcanti and Larrazábal 2004, Dias et al. 2010), the west-central Gulf of Mexico (López-Salgado et al. 2000), the eastern tropical Pacific (northwestern Mexican coast) (Suárez-Morales et al. 2000), the Mediterranean Sea and the North Atlantic (Andersen et al. 2001, 2004), and the eastern tropical Atlantic Ocean from 6°S to 4°N and at 6°W, 12°W, 18°W, and 24°W (Piontkovski et al. 2003). Small calanoids were dominant at 1 m (smaller calanoids) and large calanoids (like *C. carinatus*) at 800 m during both sampling periods. Poecilostomatoid copepods (Oncaeidae and Corycaeidae families) were more abundant than the calanoids at 1 m, 250 m, and 1,200 m. The same results were reported by Roman et al. (1993) who found the concentrations of calanoids usually decreased with depth in the tropical Pacific. Poecilostomatoids dominated the deepest stratum off Bermuda (Paffenhöfer and Mazzocchi 2003) and in the Red Sea, the Arabian Sea, and the Eastern Mediterranean Sea down to a maximum depth of 1,850 m (Böttger-Schnack 1994). Vertical- and horizontal zooplankton distributions depend on food availability and predation pressure (Fernandez-Alamo and Farber-Lorda 2006). In the present study, an abundance of calanoid suspension-feeders was reported in the chlorophyll-rich (upper) layers, whereas the detritivorous poecilostomatoids had a slightly deeper but wider distribution. Paffenhöfer and Mazzocchi (2003) hypothesize that feeding behavior determines the depth ranges that are occupied by specific genera. According to these authors, young forms and adults of a certain species occupy a flexible vertical range that meets their main needs. The major variables include temperature, food quality, food quantity, and predation.

During the rainy season, the five most abundantly identified calanoid copepod species were mainly tropical and oceanic. During the previous dry season, an abundance of neritic calanoids was noted (*C. velificatus*, *S. pileatus*, *P. quasimodo*, and *T. turbinata*) and cold water species (*C. carinatus*). These observations can be attributed to lower salinity and temperature values, respectively. Lopes et al. (1999, 2006) reported similar findings for the Rio de Janeiro coast, on the eastern continental shelf of Rio de Janeiro State and the southern Brazilian shelf, respectively, and, Dias et al. (2010) for the continental shelf of the Campos Basin.

The vertical distribution of the copepod assemblages varied due to differences in the environmental conditions along

the water column. The copepod assemblages occupied different niches at each sampling depth. Variations in the vertical distribution of the species must be considered to understand their relationships at each depth. Species-specific depth preferences and ranges created statistically distinct communities at each depth. The copepod assemblages detected at 1 m consisted mainly of tropical- and subtropical species indigenous to the tropical oceanic waters (TW) of Brazil (Cavalcanti and Larrazábal 2004, Lopes et al. 2006, Neumann-Leitão et al. 2008, Nunes and Resgalla Jr 2012). *Candacia pachydactyla*, *S. danae*, and *A. limbatus* are considered indicators at this depth. These species are epi- and mesopelagic in oceanic waters and have been detected in the tropical- and subtropical waters of the Atlantic, Pacific, and Indian Oceans (Bradford 1973, Bradford-Grieve et al. 1999, Razouls et al. 2000, 2005–2018).

In a study of the Campos Basin, Dias et al. (2010) suggested that oceanic waters influence the differences in copepod composition and abundance. Deep-water species contribute to the upper water masses. The vertical distribution of *C. carinatus* is limited to the deeper waters below the thermocline and the oxygen minimum layer (Verheye et al. 2005, Gaard et al. 2008, Teuber et al. 2013). The vertical distribution of plankton assemblages helps explain the organization and dynamics of pelagic communities and the vertical flux of organic matter throughout the water column (Nogueira-Júnior et al. 2015). Large-scale spatial patterns of certain zooplankton groups coincide with surface water masses, circulation, and upwelling regions. This coincidence aligns with the ecological and dynamic partitioning of the pelagic ecosystem (Fernandez-Alamo and Farber-Lorda 2006). Sournia (1969) indicated that such obvious seasonal changes are not always evident in tropical oceans. What does occur is a succession of small changes in plankton stocks determined by local weather conditions and water mass movements.

The parameters responsible for the signatures of the water masses sampled at each depth correlate with the separation of the copepod assemblages along the water column. The water masses at the four depths have their own hydrographic characteristics. The physicochemical parameters (salinity and temperature) were the main factors influencing copepod assemblage structure and distinction. McManus and Woodson (2012) proposed that plankton interacts with their environment across a range of scales and theorized that the spatial distributions of oceanic organisms (from the smallest plankton to the largest predators) are determined by the interactions between organism behavior and physical oceanographic structure and processes. It has been reported that in marine ecosystems, vertical stratification along the water column influences the distribution of fish larvae and zooplankton groups (Pilar Olivar et al. 2010, Nogueira-Júnior et al. 2015, Doxa et al. 2016). In this study, the model generated for the sampling period influenced the compositions of the copepod assemblages at each sampling depth.

FINAL CONSIDERATIONS

This study shows that various environmental parameters influenced the spatial patterns of copepod assemblages. This observation implies that these consortia occupy distinct niches throughout the Campos Basin. The sample grid included in this study is more extensive than that used in any previous study of the southwest Atlantic Ocean. The findings of this study helped explain the vertical distribution of the copepod species in this region.

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Supplementary material 1

Table S1. Vertical distributions of the mean, standard deviation (SD), relative abundance (RA), and occurrence frequency (OF) of the copepod species found in Campos Basin, during the rainy season.
Authors: Cristina de Oliveira Dias, Adriana Valente de Araujo, Sérgio Luiz Costa Bonecker
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Link: https://doi.org/10.3897/zoologia.35.13886.suppl1

Supplementary material 2

Table S2. Vertical distributions of the mean, standard deviation (SD), relative abundance (RA), and occurrence frequency (OF) of the copepod species found in Campos Basin, during the dry season.
Authors: Cristina de Oliveira Dias, Adriana Valente de Araujo, Sérgio Luiz Costa Bonecker
Data type: species data
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